Results of Preliminary Analyses of the Effect of Climate Change on River Herring

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Climate change and marine species

Climate change will affect the abundance and distribution of marine fishes. Analysis of historical data demonstrates that many species response by shifting their distribution poleward and into deeper waters in response to warming (Dulvy et al., 2008; Nye et al., 2009; Perry et al., 2005). Community composition can also change with a shift to warmer water species assemblages in both marine and estuarine systems (Collie et al., 2008; Howell and Auster, 2012; Lucey and Nye, 2010). Coupling of species distribution and population dynamic models with climate models also indicate that climate change will continue to affect marine populations. Using niche models, species distributions are projected to shift poleward (Cheung et al., 2008), growth is projected to decrease (Cheung et al., 2012), and population productivity is projected to decrease for cold-water species (Fogarty et al., 2007) and increase for warm-water species (Hare et al., 2010). Similar analyses have been used in a protected species framework and the general patterns described above apply. As one example, cusk in the Northeast U.S. continental was projected to shift poleward with increasingly fragmented habitat using global climate models (Hare et al., 2012).

The purpose here is to couple global scale general circulation models (GCMs) with models of river herring distribution and abundance along the U.S. east coast. Here we focus on the results of a species niche model that projects the marine distribution and abundance of river herring in the future under different scenarios of climate change. Our work with river herring will continue over the next 1-2 years and will evaluate the effect of climate change on river herring productivity and life history in both marine and freshwater habitats. To date we have focused on the marine stage of river herring, because the links between river herring biology and climate during freshwater stages are unclear. Many proposed links were identified at the River Herring-Climate Workshop hosted by NMFS Northeast Regional Office but all of these potential impacts will require more detailed investigation before the mechanisms can be coupled to climate models. Thus, our initial approach was 1) to develop climate projections for the U.S. east coast, 2) to develop a species niche model for the two species of river herring based on the NMFS Northeast Fisheries Science Center trawl survey, and 3) to project distribution in the future using an ensemble of climate models. Projections of temperature driven changes in marine distribution will provide a first-order evaluation of the effect of climate change on the marine stages of river herring.

General Climate Change projections for the Northeast US

In response to anthropogenic greenhouse gas emissions, GCMs project an increase in temperature, an increase in precipitation at higher latitudes in the Northern hemisphere, and greater frequency of extreme events at a global scale (IPCC, 2007). However, GCMs are designed to examine large scale changes in climate (greater than 100-200km) and not local or regional changes (10s of km). Thus, GCMs are often downscaled to understand the effects of climate change on a regional scale.

One such downscaling effort is the North American Regional Climate Change Assessment Program (NARCCAP). NARCCAP used multiple GCMs coupled with multiple regional climate models (RCMs) to

US Hydrologic Units (huc2)

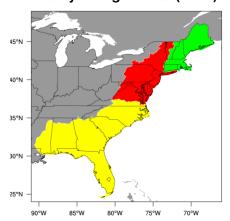


Figure 1: Regions for which mean changes in climatic variables were estimated from NARCCAP downscaling products. Regions were based on Hydrological Units at the HUC-2 scale based on regional topography.

simulate climate change over North America at a 50km resolution. More information about NARCCAP can be found at http://www.narccap.ucar.edu/. The NARCCAP simulations spanned the periods 1970-2000 (20th century) and 2038-2069 (21st century), where the latter used the A2 emissions scenario. We used six combinations of RCMs coupled with GCMs from the NARCCAP archive to understand changes in river herring habitat while they reside in freshwater systems. Changes in mean temperature, precipitation, snow melt, and runoff were obtained by calculating the differences between the 20th century and 21st century. The changes in these variables are presented as averages (or an ensemble mean) over the six GCM-RCM combinations.

Based on regional topography we calculated changes in average temperature and precipitation for 3 US Hydrological Units (Northeast US, Mid Atlantic, and South Atlantic) at the HUC2 scale to examine regional changes in temperature, precipitation

and runoff (Figure 1). The trends in mean temperature were consistent across the three regions in that temperature increased outside of the historical temperature range across seasons (Figure 2). In the Northeast US and South Atlantic, temperature increased by about 1.5°C throughout the year. In the Mid Atlantic, temperature increased by about 2°C throughout the year.

Unlike the projections of temperature change, changes in precipitation were accompanied by high variability such that an overall trend was less clear (Figure 3). There was a slight tendency for higher precipitation in winter. We examined seasonal runoff in the Northeast US and found that runoff was reduced in the spring in the Northeast and MidAtlantic. The timing of maximum flow occurred slightly earlier in the season in the Northeast likely as a result of a projected decrease in snow depth in this region (Figure 4). However, these estimates of runoff are course and are associated with high variability making the future changes in precipitation and runoff less certain than the changes in temperature.

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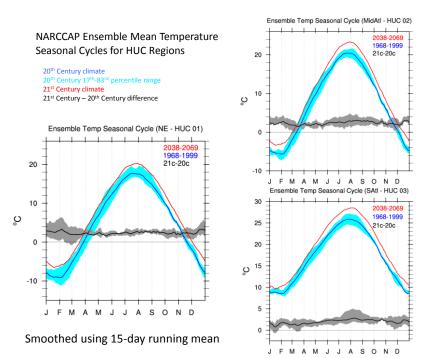
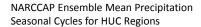
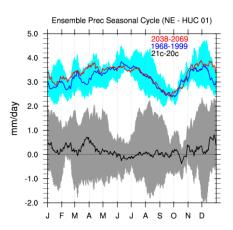


Figure 2: Ensemble means and change in temperature from NARCCAP downscaling products for 3 regions along the east coast. Blue solid lines indicate the historical mean values from 1968-1999 with turquoise shading indicating the 17-83rd percentile range. Note that the projected values for 2038-2069 are outside the ranges in nearly all cases. Black solid lines indicate the mean temperature change for each season with the standard deviation indicated by the gray shaded areas.



- 20th Century climate 20th Century 17th-83rd percentile range 21st Century climate
- 21st Century 20th Century difference



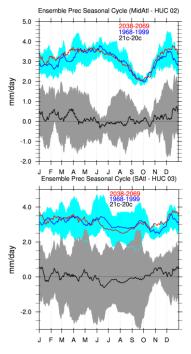


Figure 3: Ensemble means and change in precipitation from NARCCAP downscaling products for 3 regions along the east coast. Blue solid lines indicate the historical mean values from 1968-1999 with turquoise shading indicating the 17-83rd percentile range. Black solid lines indicate the mean change in precipitation with gray shading representing the variability in this estimate. Note that the high variability indicated by the turquoise and gray shading.

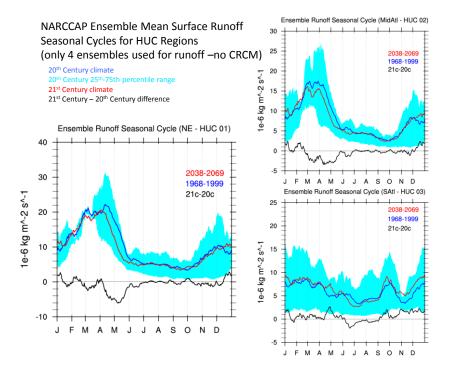


Figure 4: Ensemble means and changes in surface runoff from NARCCAP downscaling products for 3 regions along the east coast. Blue solid lines indicate the historical mean values from 1968-1999 with turquoise shading indicating the 17th to 83rd percentile range.

Despite a general increase in precipitation, runoff decreased, likely due to an increase in evaporation with higher air temperatures. The results suggest that water temperatures in the rivers will be warmer and that there will be a decrease in the river flow in the northeast and mid-Atlantic states in late winter/early spring when river herring start their migration up rivers to spawn. The reason for this

change in runoff timing in the Northeast is primarily because snow depth decreases from the historical to the projected time period.

In the marine environment, results from GCMs indicate an increase in the surface and 200m temperature over most of the ocean including the northwest Atlantic. The salinity increases over the mid-latitudes (up to ~45°N) and decreases over portions of the subarctic in the Atlantic. The temperature and salinity changes enhance the stratification in the North Atlantic, which may impede the mixing of nutrients (not included in these GCMs) into the surface waters. A different approach was

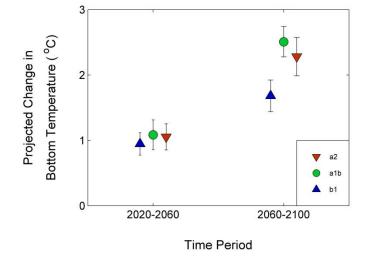


Figure 5: Projected mean temperature change (+/- 1 standard deviation) calculated from 8 GCM's for 3 different scenarios. For details see Hare et al. 2012

employed to project temperature changes in the North Atlantic. Output from 8 GCMs was averaged to create an ensemble change in temperature at 20m depth bins, 2 month time blocks for 3 broad areas over the Atlantic. Ensemble means were calculated for two future time periods; 2020-2060 and 2060-2100. Temperature in the marine realm is expected to increase by 2-3°C by the later time period 2060-2100 (Figure 5).

Effects of climate change on Blueback herring and alewife

River herring are dependent on both freshwater and marine ecosystems. Freshwater and marine ecosystems are affected by different perturbations and climate change will interact with these stressors in both habitats. Thus, to fully understand the effects of climate change on river herring we must understand how habitat in both of these environments will change in the future. While a large body of literature exists for river herring in freshwater systems, these data are collected using vastly different methodologies across river systems and for varying time periods. Many studies have been conducted, but are usually short in duration (1-2 years) and limited in geographic scope (one location within a river system). Temperature, precipitation, stream flow, predation and land use change have all been identified as stressors on river herring populations. Of these, climate will most directly affect temperature, precipitation, and the timing of peak flow, but there is little consensus and few empirical relationships to fully evaluate the effect of changes in the freshwater physical environment on river herring. Timing of the upstream migration of adult river herring, as with other anadramous fish, is thought to be triggered by temperature. Analysis of stream temperatures in New England indicate that the temperature at which alewife start their upstream migration (9°C) has occurred on average 12 days earlier since the 1970s (Ellis and Vokoun, 2011). Upstream and downstream migration can be hindered by runoff volatility; flow rates that are too high or too low could negatively impact spawning migration of adults up rivers and egress of juveniles out of rivers.

For a robust analysis of the effects of climate change on river herring in freshwater systems, a major effort to model historical and future stream flows and temperature is needed in river systems where run counts and/or juvenile surveys have simultaneously occurred for time periods long enough to understand the impacts of temperature and flow on these species. Participants at the NMFS Northeast Regional Office presented efforts ongoing at USGS to model flow and temperature in freshwater systems. Using these models they have projected the effects of climate change in several watersheds around the country. As a result of the workshop we are collaborating with USGS partners to model river systems important to river herring in the Northeast US. Empirical relationships between physical variables and river herring population indices are being developed for the Connecticut and Thames Rivers in Connecticut where models of stream flow and temperature are being developed. Colleagues at USGS are using an established hydrological model called Precipitation Runoff Modelling System (PRMS) in combination with a temperature model (SNTemp) to predict historical and future temperature and river flow for these rivers. Should our efforts in the Connecticut River be successful, other river systems could be modeled along the East Coast for which there is better data for river herring.

At this point our analysis will focus on river herring thermal habitat in the marine environment using NOAA NMFS NEFSC trawl survey data that has been collected consistently in both coastal and offshore

strata since the 1970s. It is often pointed out the name "river herring" is appropriate only in comparison to sea herring as alewife and blueback herring spend the majority of their lives in the ocean. Thus, changes in marine habitat will greatly impact the coastwide population. Survey catches of river herring are more evenly distributed across the continental shelf in spring, and concentrated in more northern areas such as the Gulf of Maine, Georges Bank, and Canadian waters during the summer, fall, and winter.

Previous analysis of alewife spring distribution from 1968-2007 indicated that this species had shifted its distribution in a manner consistent with what would be expected with climate change. That is, their center of distribution shifted northward in the NEFSC trawl survey area and they were found at deeper depths (Nye et al., 2009). The minimum latitude of occurrence had also shifted north indicating a northward shift in their range and the overall area occupied increased indicating that although this species had shifted its distribution northerly, it was found at an increasing number of stations in the northern part of its range. A reanalysis of both alewife and blueback herring using data from 1975-2012 confirms that both alewife and blueback herring have shifted their distribution to more northerly waters in the spring. In the fall, blueback herring has shifted northward, but alewife has not. These shifts can be seen in maps in 6 year time blocks (Figures 6-7). Although we analyzed data from both fall and spring, the probability of catch was much higher in spring than in the fall survey so we will discuss the results of our analyses using the spring trawl survey data.

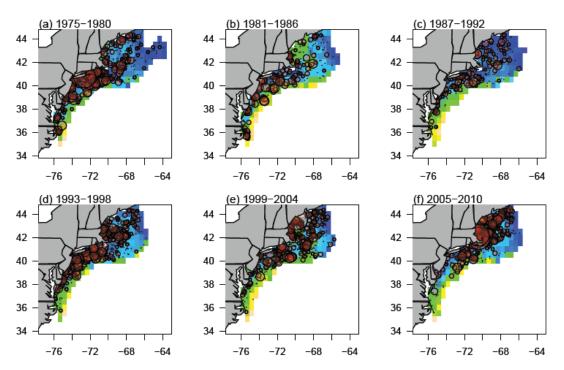


Figure 6: The catch distribution of alewife from the NEFSC bottom trawl survey. Catches are aggregated over six-year time blocks and the size of the circle corresponds to the number of alewife caught per station. Temperature is represented by the shading from blue (cold water) to red (warm water).

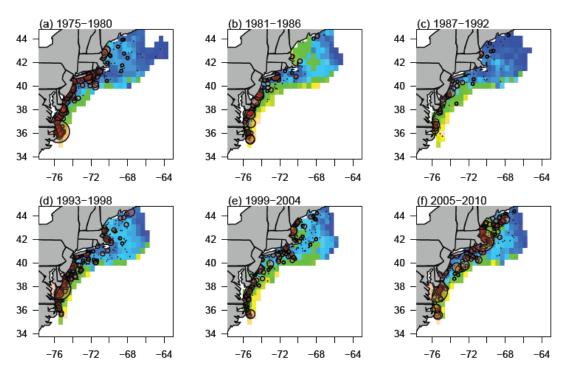


Figure 7: The catch distribution of blueback herring from the NEFSC spring bottom trawl survey. Catches are aggregated over six-year time blocks, and the size of the circle corresponds to the number of blueback caught per station. Temperature is represented by the shading from blue (cold water) to red (warm water).

That the observed shifts in distribution are in response to warming water temperatures is supported by the observation that blueback herring and alewife exhibited preference for water of a certain temperature while in the marine realm. Both blueback herring and alewife prefer temperatures between 3-7°C in the spring. Based on analysis in the fall, blueback appear to prefer bottom temperatures between 9-11°C while alewife prefer cooler temperatures in the 4-11°C range. The total habitat within the temperature range *preferred* by alewife and blueback herring in spring is projected to decrease under future climate predictions (Figure 8). Alewife and blueback herring may shift their distribution as a consequence of the reduction in optimum habitat; however, the realized change in distribution and population size will also be related to other stressors on the populations, such as fishing and habitat destruction in the freshwater environment and the ability of these fish to adapt to suboptimal marine habitat.

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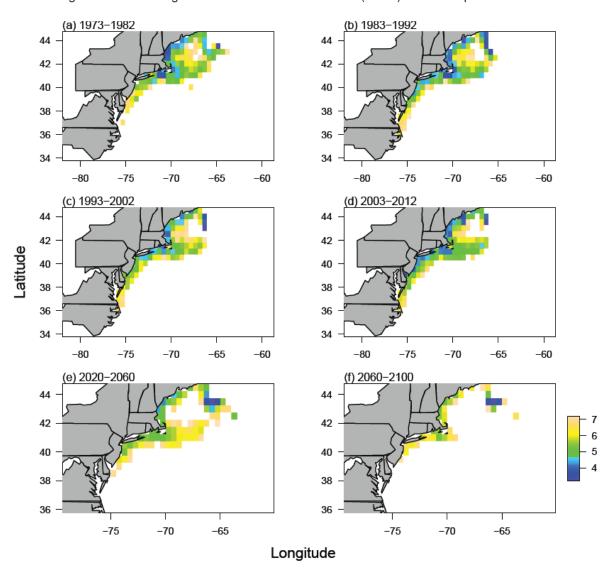


Figure 8: Spatial distribution of bottom temperature within the preferred temperature range (3-7°C) of alewife and blueback herring in the spring. Waters within this temperature range are inferred to be good habitat for river herring based on the quotient analysis. Areas without color coding are outside the preferred temperature range.

To quantify the effects of climate change on river herring populations, we used Generalized Additive Models (GAMs) using an approach similar to Hare et al. (2012). GAMs are a flexible modeling technique and are particularly useful when the relationship between variables is unknown and potentially complex and non-linear. We considered the inclusion of many potential variables in the GAMs including sea surface temperature (SST), bottom temperature (BT), year, depth, salinity, solar elevation, broadscale climate indices (AMO, NAO, etc.) and population size. Many of these variables were excluded from the analysis. Broadscale climate indices were not correlated with alewife and blueback herring abundance or distribution. From a physiological point of view, we excluded depth and salinity because these factors are probably not major drivers of river herring distribution. Depth is unlikely to be important for a

pelagic fish and salinity changes very little in the marine area that we modeled. Furthermore, because river herring undergo migrations between freshwater and marine waters they have a tremendous ability to compensate for changes in salinity. Richkus (1974) found that juvenile and adult alewives that were transferred from freshwater to saline water (32 ppt), and vice versa, experienced zero mortality. Leim (1924) noted that alewife migrate as far upstream as they can travel and concluded that alewife may be less dependent on saltwater than other diadramous fish such as American shad. Furthermore, some populations of alewife have become landlocked and are not at all dependent on saltwater (Greene et al., 2009; Scott and Crossman, 1973). Similarly, the eggs and larvae of blueback herring can survive in salinities as high as 18 to 22 ppt even though spawning occurs in freshwater (Johnston and Cheverie, 1988).

Climate change projections in the marine environment were used from Hare et al. (2012). An ensemble of eight GCM's with ocean resolutions of less than 2° were chosen to maximize the resolution of shelf bathymetry and dynamics. Most of the variability in temperature change projections stemmed from the individual climate models and the time period of the projections (2020-2060 and 2060-2100). The ensemble approach averages across the inter-model variability and the examination of the two broad time periods accounts for the strong influence of climate variability on changes in mean temperature. The 'delta' method was used to project future surface and bottom temperatures such that the ensemble mean change in temperature represented as a regional delta value was applied to an historical climatology (1977-2009). There was relatively little variability in the projected temperature change associated with region, depth and season. Although changes in temperature were calculated for 3 emission scenarios (B1, A1B, and A2), we projected future river herring habitat and abundance using the moderate emission (A1B) scenario (Figure 5).

The final alewife model was a negative binomial GAM with Year as a factor and smooths of SST, BT, and the SST:BT interaction (Figure 9). We considered modeling spatial and temporal correlation, but objective analyses indicated that it was not necessary to include autocorrelation. Alewife abundance (number per tow) decreased with surface temperature, but was not affected as greatly by bottom

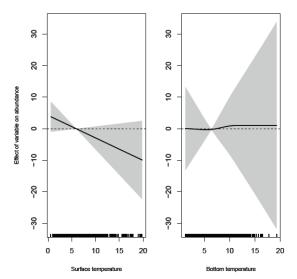


Figure 9: Effect of surface (left) and bottom (right) water temperature on alewife abundance distribution

temperature.

Using the GAM, projections of alewife distribution and abundance can be predicted for each year, but for ease of interpretation, two years of low and high relative abundance were chosen to illustrate the effects of population abundance and temperature on alewife distribution. The low and high abundance years were objectively chosen as the years closest to -1 and +1 standard deviation from overall mean abundance. Spatial projections of abundance were limited to the spatial extent of the survey in the low and high abundance years. At low population size,

alewife abundance is projected to decrease throughout the Northeast US shelf particularly in the MidAtlantic and Southern New England (Figure 10). The model predicts less suitable habitat with patchy areas of high density in the Gulf of Maine and Georges Bank in 2060-2100. The coastwide abundance estimate decreases (Figure 11). At high population size, abundance is projected to increase slightly in the near term (2020-2060), but is projected to decrease and become more patchy in 2060 – 2100 (Figures 10, 11). The changes in abundance due to warming associated with climate change are +4.64% for the time period 2020-2060 and -39.14% the decline in 2060-2100.

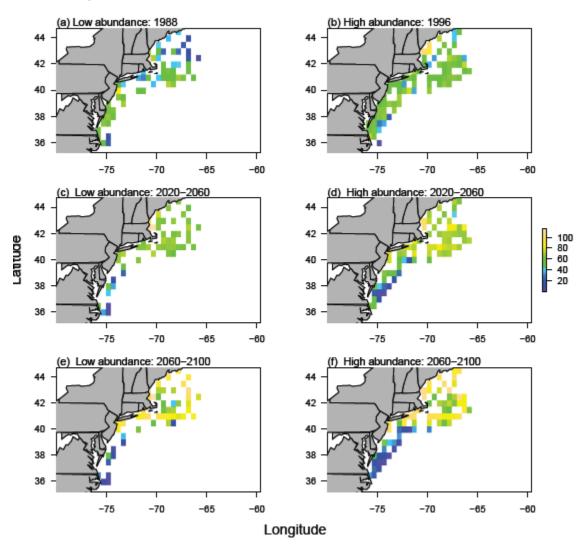


Figure 10: Alewife abundance (number per tow) as estimated by the GAM depicted spatially for low abundance (a,c,e) and high abundance (b,d,f)

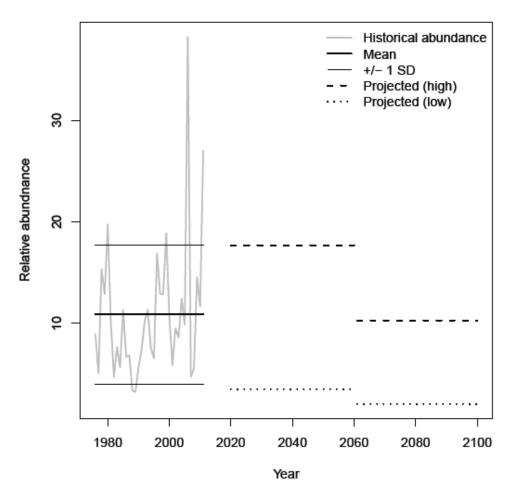


Figure 11: Relative abundance of alewife estimated by the GAM starting with high population size (dashed lines) and low population size (dotted lines). High and low population estimates are based on abundance at +1 and -1 standard deviation of overall mean abundance.

For blueback herring, the final model was a negative binomial GAM with Year as a factor and smooths of SST, BT, and the SST:BT interaction (Figure 12). Once again, it was not necessary to include autocorrelation. Blueback abundance (number per tow) decreased with surface and bottom temperature. Two years closest to the -1 and +1 standard deviation from mean population abundance were selected to reflect the combined effect of warming with low and high abundance of blueback herring. The GAM was then used to project the spatial distribution and abundance of blueback herring. At both high and low population size, blueback herring abundance is projected to increase throughout the Northeast US especially in the MidAtlantic and Georges Bank (Figure 13). Population abundance is projected to increase at both high and low abundance scenarios (Figure 14). However, at low abundance the increase is minimal and remains at a level below the long term mean. The percentage change due to climate change (only temperature) is +29.93% for the time period 2020-2060 and +55.81% for 2060-2100.

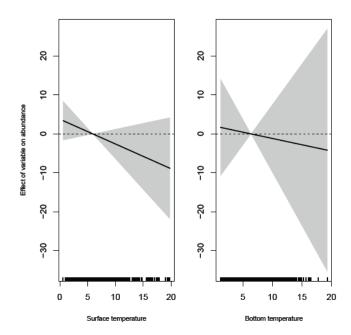


Figure 12: Effect of Surface temperature and bottom temperature on Blueback herring abundance in the GAM

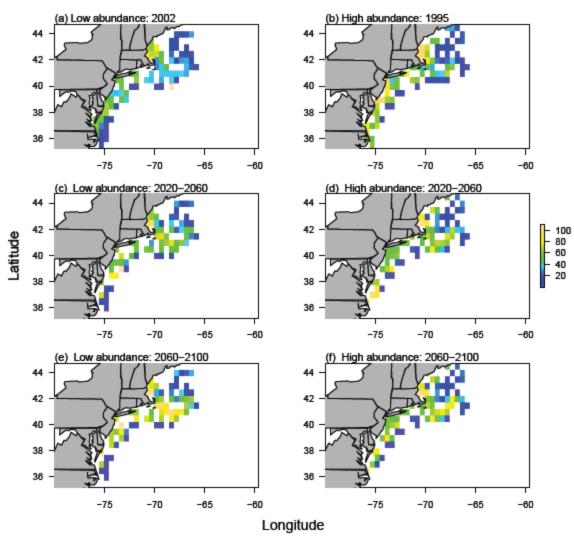


Figure 13: Spatial depiction of blueback herring abundance (number per tow) as predicted by the GAM for low abundance (a,c,e) and high abundance (b,d,f) scenarios.

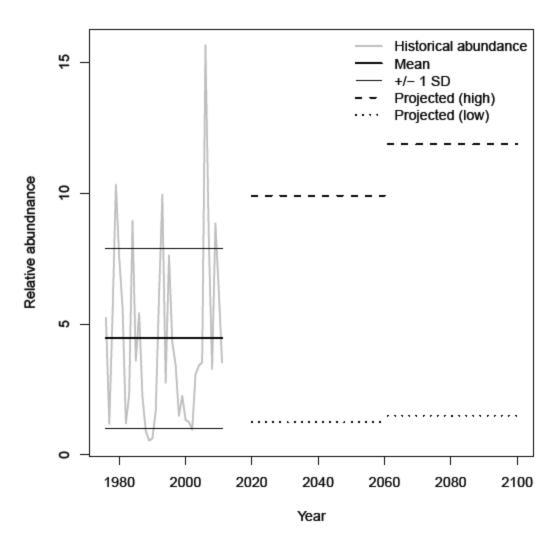


Figure 14: Projected abundance of blueback herring at high (dashed lines) and low (dotted lines) for two time periods

Conclusions

Our research indicates that climate change and specifically warming will cause river herring preferred marine habitat to shift northward. As a consequence river herring populations at the southern extent of their range will be negatively affected as the distance between optimal marine habitat and natal spawning habitat increases. This mismatch will have negative population level effects and cause population declines in southern rivers resulting in an observed shift in distribution. Shifts in marine distribution in response to warming have already been observed in these species. Our projections of river herring abundance emphasize the importance of population size in projected future river herring abundance and distribution. At low population sizes and warming water temperatures, alewife populations decline and blueback herring populations remain below the 40-year mean. At high population sizes, alewife population abundance declines, but blueback herring abundance increases. The difference in species response may reflect the different temperature tolerances (9-11°C for

blueback herring and 4-11°C for alewife) and as indicated by the southern limit of their ranges. Blueback herring may be able to tolerate higher temperature as its range extends as far south as Florida, but the southern extent of the alewife's range is limited to North Carolina. For both species, our analysis indicates that if robust populations of these species are maintained that declines due to the effects of climate change will be reduced.

The results presented here are a first order evaluation of the effect of climate change on river herring. We have only examined the marine component of the life cycle, but we are starting to develop models and projections for the freshwater component. Additionally, our approach only evaluates the direct effect of warming marine water temperatures on river herring and does not consider stratification, trophic interactions and other stressors that, in addition to their direct effects, interact with climate change. River herring have been subject to many stressors including impoundments, poor water quality and overall reduction in habitat in freshwater systems (Hall et al., 2011; Hall et al., 2012) as well as directed fishing and bycatch throughout its range (Limburg, 1996). Climate is an important driver of river herring population dynamics, but it may not be the most dominant driver and the way in which climate interacts with these other stressors is largely unknown.

Works cited

Cheung, W.W.L., Close, C., Lam, V.W.Y., Watson, R., Pauly, D., 2008. Application of macroecological theory to predict effects of climate change on global fisheries potential. Marine Ecology Progress Series 365, 187-197.

Cheung, W.W.L., Sarmiento, J.L., Dunne, J., Frolicher, T.L., Lam, V.W.Y., Deng Palomares, M.L., Watson, R., Pauly, D., 2012. Shrinking of fishes exacerbates impacts of global ocean changes on marine ecosystems. Nature Clim. Change advance online publication.

Collie, J.S., Wood, A.D., Jeffries, H.P., 2008. Long-term shifts in the species composition of a coastal fish community. Canadian Journal of Fisheries and Aquatic Sciences 65, 1352-1365.

Dulvy, N.K., Rogers, S.I., Jenning, S., Stelzenmuller, V., Dye, S.R., Skjoldal, H.R., 2008. Climate change and deepening of the North Sea fish assemblage: a biotic indicator of warming seas. Journal of Applied Ecology 45, 1029-1039.

Ellis, D., Vokoun, J.C., 2011. Earlier spring warming of coastal streams and implications for alewife migration and timing. North American Journal of Fisheries Management 29, 1584-1589.

Fogarty, M.J., Incze, L., Hayhoe, K., Mountain, D.G., Manning, J., 2007. Potential climate change impacts on Atlantic cod (*Gadus morhua*) off the northeastern USA. Mitigation and adaptation strategies for Global Change 13, 1573-1596.

Authro, 2009. Fish Habitat: A review of utilization, threats, recommendations for conservation, and research needs. Washington, DC.

Hall, C.J., Jordaan, A., Frisk, M.G., 2011. The historic influence of dams on diadramous fish habitat with a focus on river herring and hyrological longitudinal connectivity. Landscape Ecology 26, 95-107.

Hall, C.J., Jordaan, A., Frisk, M.G., 2012. Centuries of anadramous forage fish loss: consequences for ecosystem connectivity and productivity. Bioscience.

Hare, J.A., Alexander, M.A., Fogarty, M.J., Williams, E.H., Scott, J.D., 2010. Forecasting the dynamics of a coastal fishery species using a coupled climate-population model. Ecological Applications 20, 452-464.

Hare, J.A., Manderson, J.P., Nye, J.A., Alexander, M.A., Auster, P.J., Borggaard, D.L., Capotondi, A.M., Damon-Randall, K.B., Heupel, E., Mateo, I., O'Brien, L., Richardson, D.E., Stock, C.A., Biegel, S.T., 2012. Cusk (Brosme brosme) and climate change: assessing the threat to a candidate marine fish species under the US Endangered Species Act. ICES Journal of Marine Science: Journal du Conseil 69, 1753-1768.

Howell, P., Auster, P., 2012. Phase shift in an estuarine finfish community associated with warming temperatures. Marine and Coastal Fisheries *in press*.

IPCC, 2007. Climate Change 2007: Synthesis Report. Contribution of Working Groups I, II and III, in: Team, C.W., RPachauri, R.K., Reisinger, A. (eds.), Fourth Assessment Report of the Intergovernmental Panel on Climate Change, Geneva, Switzerland, p. 104.

Johnston, C.E., Cheverie, J.C., 1988. Observations on the diel and seasonal drift of eggs and larvae of anadromous rainbow smelt, Osmerus mordax, and blueback herring, Alosa aestivalis, in a coastal stream on Prince Edward Island. Canadian Field Naturalist 102, 508-514.

Leim, A.H., 1924. The life history of the shad (Alosa sapidissima) (Wilson) with special reference to the factors limiting its abundance. Biological Board of Canada, Contribution to Canadian Biology 155.

Limburg, K.E., 1996. Modelling the ecological constraints of growth and movement of juvenile American Shad (Alosa sapidissima) in the Hudson River Estuary. Estuaries 19, 794-813.

Lucey, S.M., Nye, J.A., 2010. Shifting species assemblages in the northeast US continental shelf large marine ecosystem. Marine Ecology Progress Series 415, 23-33.

Nye, J.A., Link, J.S., Hare, J.A., Overholtz, W.J., 2009. Changing spatial distribution of fish stocks in relation to climate and population size on the Northeast United States continental shelf. Marine Ecology Progress Series 393, 111-129.

Perry, A.L., Low, P.J., Ellis, J.R., Reynolds, J.D., 2005. Climate change and distribution shifts in marine fishes. Science 308, 1912-1915.

Richkus, W.A., 1974. Factors influencing the seasonal and daily patterns of alewife (Alosa pseudoharengus) migration in a Rhode Island river. Journal of the Fisheries Research Board of Canada 31, 1485-1497.

Scott, W.B., Crossman, E.J., 1973. Freshwater fishes of Canada. Fisheries Research Board of Canada Bulletin 184.